Basidiomycetes of the Greater Antilles Project 4

D.J. Lodge,[1] T.J. Baroni[2] and S.A. Cantrell[1]

[1]*Center for Forest Mycology Research, Forest Products Laboratory, USDA-Forest Service, PO Box 1377, Luquillo, PR 00773-1377, USA;* [2]*Department of Biological Sciences, SUNY Cortland, PO Box 2000, Cortland, NY 13045, USA*

Introduction

The inventory of basidiomycetes of the Greater Antilles, with special emphasis on the Luquillo Long-Term Ecological Research Site, was a 4 year project initiated in 1996 with funding from the USA National Science Foundation's (NSF) Biotic Surveys and Inventories Program.* The objective was to survey and inventory all basidiomycetes except rust fungi on the Caribbean islands of Puerto Rico, the Virgin Islands, Hispaniola and Jamaica. Although Cuba was not visited, historical records from there have been included in the analyses.

Basidiomycetes, except for those with durable basidiomes such as *Lentinus* spp. and polypore fungi, were poorly known in the Greater Antilles before the project began. The Caribbean was colonized five centuries ago and many botanists of early date collected hard polypores since the basidiomes retained their characteristics sufficiently for later identification. Although Stevenson (1970) had summarized all the previous records of fungi from Puerto Rico and the nearby Virgin Islands, he listed only 55 species of ephemeral basidiomycetes (Lodge, 1996a). Lodge (1996b) added 170 ephemeral basidiomycetes to the list for Puerto Rico, of which 10–30% from various families were previously undescribed species. Ciferri (1929) listed only 14 species of agarics and nine species of gasteromycetes among the 63 macrobasidiomycete species known from the

*The Forest Products Laboratory in Madison is maintained in cooperation with the University of Wisconsin, while the laboratory in Puerto Rico is maintained in cooperation with the USDA-Forest Service International Institute of Tropical Forestry. This article was written and prepared by a US Government employee on official time, and the information is therefore in the public domain and not subject to copyright.

© CAB *International* 2002. *Tropical Mycology*, Vol. 1, *Macromycetes* (eds R. Watling, J.C. Frankland, A.M. Ainsworth, S. Isaac and C.H. Robinson)

Dominican Republic on the island of Hispaniola, whereas 35 were species of polypores and other aphyllophoroid fungi. Benjamin and Slot (1969) summarized the fungi known from Haiti on Hispaniola based on specimens deposited at Beltsville, Maryland, including two species not recorded by Ciferri (1929). A parataxonomist recently added 19 new records of agaric species from the Dominican Republic (Rodríguez Gallart, 1989, 1990, 1997) but corresponding voucher collections were not located in the National Herbarium.

The basidiomycete fungi in Jamaica and Cuba had received somewhat more attention than those in Puerto Rico and Hispaniola. Swartz (1788) collected and described several species of polypores from Jamaica, and Hennings (1898) described three more species collected by Lindau. Murrill (1910, 1911a, b, c, d, 1915, 1920a,b, 1921a,b) collected in Jamaica in the early 1900s and described many new species. In addition, Dennis (1950, 1953) had made one bountiful collecting trip to Jamaica. Ryvarden (1985) revised the polypores described by Murrill, and the *Hygrophoraceae* were included in Hesler and Smith's (1963) monograph. Despite these efforts, the basidiomycetes of Jamaica remained poorly known, many represented by a single collection. Historically, the basidiomycetes of Cuba had received almost as much attention as those in Jamaica. Collections by Charles Wright were described by Berkeley and Curtis (1868) and revised by Murrill (1911a, b, c, d); Dennis (1950, 1951a, b, c); Pegler (1983), Ryvarden (1984) and Hjortstam (1990). Earle (1906) collected widely in Cuba in the early 1900s; he described some species in 1906 and 1909, but sent many others on to W.A. Murrill, who revised and described them with other West Indian, Honduran and Mexican collections (1911a, b, c, d).

Investigators in the course of this survey and inventory of basidiomycetes in the Greater Antilles have discovered at least 75 new species and varieties so far, as well as several new genera and one possible new family or order. In this chapter, the percentages and numbers of new taxa are compared with original estimates. Problems encountered in classifying some of the collections, and some surprising results from DNA analyses that were used to resolve their placement are also discussed. Some of the biogeographic patterns that have emerged are also shown.

Predicted versus Observed New Species

Methods for generation of predicted values

Predictions of the number of new species that have yet to be discovered are generally based on the previous rate of discovery. The percentage of expected species in each family was assumed to be the same as in the recent data from Puerto Rico (1983–1995; Lodge, 1996b).The expected total number of species for each family was calculated using the proportional overlap in species composition between what was known in the Greater Antilles and the better known mycotas from south-eastern USA, the Lesser Antilles (Pegler, 1983), Venezuela and Trinidad (Dennis, 1953,1970), multiplied by the number of species reported from those areas.

Duplications were eliminated in cases where the same species occurred in both comparative mycotas before the expected number of species were tallied. In the *Hygrophoraceae* for example, 17 species were known from Puerto Rico (those in Lodge, 1996b except *Hygrocybe unicolor* Pegler) of which one was known from south-eastern USA (Hesler and Smith, 1963). The monograph of Hesler and Smith (1963) listed 49 species of *Hygrocybe*, *Camarophyllopsis* and *Cuphophyllus* found in south-eastern USA, excluding species in common with the Lesser Antilles, Trinidad and Venezuela. It was expected that 5.9% (1/17) of these 49 would eventually be found in the Greater Antilles, namely two in addition to the one species already known. For the Lesser Antilles, Trinidad and Venezuela 38 species are known (Dennis, 1970; Pegler, 1983), of which ten were recorded from Puerto Rico (Lodge, 1996b). It was expected that 58.8% (10/17) of the 38 southern Caribbean species would eventually be found in the Greater Antilles, namely 12 in addition to the ten already known. A total of 23 species of *Hygrophoraceae* were known from the Greater Antilles: one (*Hygrocybe cantharellus* (Schw.) Murrill) from Jamaica and south-eastern USA (Dennis, 1953; Hesler and Smith, 1963), five known only from Jamaica or Cuba (Murrill, 1911c; Hesler and Smith, 1963) and 17 from Puerto Rico (Lodge, 1996b). The expected total number of described species of 37 was obtained as the tally of 23 species already recorded from the Greater Antilles, an additional two from North America and an additional 12 from the southern Caribbean. The percentage of expected new species was assumed to be the same as previously (23.5%). Thus, the total number of expected species (X = 48) and the number of undescribed species (Y = 11) were estimated by solving the following simultaneous equations:

$$37 \text{ known species} + \text{undescribed species } (Y) = \text{total number of species } (X) \quad (1)$$

$$Y/X = 0.235 \quad (2)$$

The expected numbers of species (total and undescribed) in the *Entolomataceae* for the Greater Antilles were generated from species already recorded (Berkeley and Curtis, 1868; Murrill, 1911d; Hesler, 1967; Lodge, 1996b) and the comparative mycotas in south-eastern North America (Hesler, 1967) and the Lesser Antilles, Trinidad and Venezuela (Dennis, 1970; Pegler, 1983). The expected number of polypores (*sensu lato*) was generated in the same way, using polypore mycotas in Venezuela (Dennis, 1970) and south-eastern North America (Gilbertson and Ryvarden, 1987), but the percentage of undescribed species was based on an 'expert guess'.

Results

Total numbers of species and new species

Progress in classifying the nearly 5000 collections generated by the project varied among families. Therefore, total numbers of species and new species could be compared with original predictions only for polypores, *Hygrophoraceae* and *Entolomataceae* (Table 4.1). Several publications

documenting additions to the mycota of the Greater Antilles followed as a result of this project, including polypores (Decock and Ryvarden, 2000; Ryvarden, 2000a, b, c, 2002), the *Corticiaceae* (Lodge, 1996b; Nakasone *et al.*, 1998), the *Hygrophoraceae* (Cantrell and Lodge, 2000, 2001), the *Entolomataceae* (Baroni and Lodge, 1998), and the *Amanitaceae*, *Boletaceae* and *Russulaceae* (Miller *et al.*, 2000).

The number of species of polypores found in the Greater Antilles was 22% more than the original estimate (Table 4.1). While at least ten unexpected representatives of African or palaeotropical species were found, the latter represented only a quarter to a third of the 38 polypore species that were in excess of the original estimate (Table 4.1). Species that are common in Africa or Asia and are rarely represented in the Greater Antilles and the Neotropics included *Abundisporus fuscopurpureus* (Jungh.) Ryv., *Cerrena meyenii* (Kl.) Hansen, *Flavodon flavus* (Kl.) Ryv., *Fomitopsis dochmius* (Berk.) Ryv., *Lenzites acuta* Berk., *Navisporus floccosus* (Bres.) Ryv., *Trametes cingulata* Berk., *Trichaptum byssogenus* (Jungh.) Ryv. and *Trichaptum durum* (Jungh.) Corner. All but one of the previously undescribed species of polypores from the Greater Antilles had ephemeral basidiomes. However, fewer new polypore species were found than expected (Table 4.1), so this cannot explain why more species of polypores were found than predicted. One contributing factor in the original underestimate could have been that the reference mycotas were incomplete. The plot-based methods which are more commonly used to project the total number of species in an area also produce underestimates (Schmit *et al.*, 1999).

The number of species in the *Hygrophoraceae* found in the Greater Antilles was also 40% more than estimated using the same methods as for polypores (Table 4.1), and the number of undescribed species was slightly higher than expected (Table 4.1), but this can explain only six of the 17 species in excess of the authors' original estimate for the *Hygrophoraceae*. The percentages of undescribed species recorded before (23.5%; Lodge and Pegler, 1990; Lodge, 1996b) and after the Basidiomycetes of the Greater Antilles Project (26%; Cantrell and Lodge, 2000a, b) were not very different. Thus, it appears that while the methods used yielded predictions for the total number of species that were in the right range, they were lower than the observed values.

Table 4.1. Predicted versus observed total numbers of species and numbers of previously undescribed species in the Greater Antilles.

Group	Total number of species predicted	Total number of species found	Expected number of new species	Observed number of new species
Polypores	170	208	10	6
Hygrophoraceae	48	63	11	17
Entolomataceae	88	89+	30	28+

Percentage of undescribed species

The percentages of new species before and after the inventory began could be compared for polypores, agarics and boletes in Puerto Rico based on partial results (Table 4.2). Only taxa that were classified to species or listed as undescribed species were included in this analysis, so the total number of agaric species for the island are likely to be at least two to five times higher. The predicted percentages of undescribed species were remarkably similar to the observed percentages in Table 4.2.

The percentage of undescribed species revealed in a survey could be expected to decline eventually as an inventory for the area nears completion. It was thought, therefore, that the percentage of undescribed species would decrease from the percentage observed in the 12 years prior to the project. This did not occur, suggesting that the inventory was not complete. The tendency for mycologists to work first on the obviously new and interesting species may bias the percentages of undescribed species and keep them unnaturally high. A significant decline in the percentage of new species, however, did not occur even among the groups of agarics that had been analysed completely (i.e. *Hygrophoraceae* 27%; and in the *Entolomataceae*, *Alboleptonia* 45% and *Pouzarella* 83%).

Problems and Surprising Results in Systematics

Several different types of problem were encountered in classifying the basidiomycetes collected in the survey of the Greater Antilles. Some of the problematic species were well known but were obviously placed in an incorrect genus. In addition, some of the new species were readily placed in existing genera but had no obvious close relatives. Other fungi were taxonomically anomalous, and belonged to none of the previously described genera.

Species previously placed in the wrong genus

For some of the previously named species found in the Greater Antilles that had been placed in the wrong genus, it was not immediately obvious where they

Table 4.2. Predicted versus observed percentages of previously undescribed species in Puerto Rico before and after the Basidiomycetes of the Greater Antilles Project. Predicted percentages of new species in the *Agaricales* and *Boletales* taken from the rate of discovery of new species in the preceding 10 years.

Group	Total number of species determined	% undescribed species	Predicted % undescribed species
Agaricales and *Boletales*	325	22	22
Polypores, *sensu lato*	118	4	6

belonged on the basis of morphological characteristics alone, but ribosomal DNA sequencing by R. Vilgalys and J.-M. Moncalvo (see Acknowledgements) was instrumental in classifying them correctly. One such example was *Collybia aurea* (Beeli) Pegler, a gregarious, lignicolous species that was originally described in the genus *Marasmius*. The pileipellis of this brilliant mustard yellow species is a cutis of repent hyphae with scattered, simple, clavate, upturned terminal elements (Pegler, 1983). Neither the coloration (Legon, 1999, Fig. 6) nor the pileipellis structure is typical of either *Marasmius* or *Collybia*, or of any of the segregate genera. Vilgalys and Moncalvo found that the ribosomal DNA sequences of *C. aurea* lined up with species in the genus *Tricholomopsis* (R. Vilgalys, Durham, North Carolina, USA, 1999, personal communication). In retrospect, this placement was logical, but it was not a solution that was even considered before the DNA sequences resolved the problem. *Marasmius rhyssophyllus* Mont. (syn. *Dictyoploca rhyssophylla* (Mont.) Baker & Dale) was another misclassified species resembling *C. aurea* in colour, habit, and pileipellis structure but differing in distant and highly intervenose lamellae (Legon, 1999, Fig. 7). It also belonged in *Tricholomopsis* according to the ribosomal DNA evidence (J.-M. Moncalvo, Durham, North Carolina, USA, 2000, personal communication).

Another species in the West Indies that had clearly been placed in the wrong genus and was previously referred to as *Tricholoma pachymeres* (Berk. & Br.) Sacc. was provisionally identified as saprobic *Tricholoma titans* H.E. Bigelow & Kimbr. The molecular data, microscopic characters, especially the lack of siderophilous granulation in the basidia and the abundance of clamp-connections, and ecological information led to the erection of *Macrocybe* Pegler & Lodge for this and related tropical species (Pegler *et al.*, 1998). More recent work indicated that *Macrocybe* did not cluster in either the *Tricholoma* or *Calocybe* clades (Moncalvo *et al.*, 2000).

Expanding the limits of described sections, subgenera and genera

The most interesting ectomycorrhizal species found was an *Amanita* in the subgenus *Amanita*. It is characterized by having two layers of universal veil that differ in colour and texture. The outer layer is thin, white and membranous with large pyramidal warts situated in the sculptured depressions of the pileus. The inner universal veil is powdery and rusty brown, covering the entire basidiome and separating from the lower side of the partial veil as a false annulus (Cantrell *et al.*, 2001, Fig. 6). The powdery veil also sloughs off the surface of the pileus, which becomes shiny and has an orange tint. There are some species with composite universal veils in the subgenus *Lepidella*, but the two veil layers are usually the same colour. O.K. Miller Jr (Blacksburg, Virginia, USA, 2000, personal communication) has not found any species in subgenus *Amanita* that is closely related to this new *Amanita* from the Dominican Republic (Miller and Lodge, 2001). *Amanita* species from the Dominican Republic have been described by Miller and Lodge (2001).

The authors are describing a new species of *Callistodermatium* Singer. This previously monotypic genus was described by Singer from South America, and differs from a related genus, *Cyptotrama*, in having pileus pigments that change colour with alkaline solutions, somewhat larger spores, and a terrestrial rather than lignicolous habit. While the type species *Callistodermatium* is dull brown, the new species found in Puerto Rico and the Dominican Republic has a pileus that was bright orange-yellow, turning fuchsia pink rather than violet in KOH (see Cantrell *et al.*, 2001, Fig. 2).

The limits of *Hygrocybe* section *Firmae* have been greatly altered by the new species discovered during the Basidiomycetes of the Greater Antilles Project (Cantrell and Lodge, 2001). Two of the new species, *Hygrocybe cinereofirma* S.A. Cantrell, Lodge, & Baroni, and *Hygrocybe brunneosquamosa* Lodge & S.A. Cantrell are dull grey and grey-brown in colour, which is very unusual for section *Firmae*. All the previously known members of this section have at least some red, yellow, green or purple coloration. *H. brunneosquamosa* is also the only member of the section with squarrose scales on the pileus (Cantrell *et al.*, 2001, Fig. 3). In addition, all the previously described species in section *Firmae* have a broadly convex or centrally depressed pileus, whereas three of the new species (*H. cinereofirma*, *Hygrocybe flavocampanulata* S.A. Cantrell & Lodge, and *Hygrocybe laboyi* S.A. Cantrell & Lodge) have a pileus disk that is umbonate or cuspidate. Previously, all the species in section *Firmae* except *Hygrocybe hypohaemacta* (Corner) Pegler had broadly attached lamellae; in this project, two new species with strongly adnexed lamellae (*H. flavocampanulata*, and *H. cinereofirma*; Cantrell and Lodge, 2001) were described.

Interesting new sections, genera and families

One of the most exciting finds on the island of Jamaica was a gregarious, greenish blue mycenoid species identified as *Clitocybula azurae* Singer (Cantrell *et al.*, 2001, Fig. 7). The dextrinoid stipe context, slightly dextrinoid lamellar trama hyphae, umbonate rather than umbilicate shape of the pileus, and the unusual greenish blue colour of the basidiomes in *C. azurae* are characteristics that are not shared with typical species of *Clitocybula*, which suggested that *C. azurae* was misplaced. *C. azurae* resembles a *Mycena* species in having amyloid spores, dextrinoid stipe tissue, and a mycenoid structure in the lower pileus and upper lamellar contexts, but the unornamented pileipellis hyphae and cheilocystidia, greenish blue rather than purplish pigments, absence of a mycenoid structure in the hypoderm, and absence of a separation zone between the stipe and pileus context suggested that it should not be placed in the genus *Mycena*. It is uncertain where this unusual species will eventually be classified. Many of the undescribed true *Mycena* species from the Caribbean also do not fit into any of the currently described sections. Another agaric with unknown affinities is a species called the 'nail-head fungus' because of its shape, dark colours and tough

texture (Cantrell *et al.*, 2001, Fig. 9). Although this species somewhat resembles *Tephrocybe*, it lacks siderophilous granulation in the basidia, and therefore appears to belong in the tribe *Tricholomatae* rather than *Lyophyllae*, and may be an undescribed genus.

A new ochraceous coloured species of *Gloeocantharellus* was discovered on the island of Tortola in the British Virgin Islands. The ribosomal DNA sequences showed that it was basal to the *Gomphaceae*, consistent with *Gloeocantharellus* (J. Spatafora, Liverpool, UK, 2000, personal communication). Another unusual discovery was an undescribed *Dichopleuropus*-like fungus (D. Reid, West Sussex, UK, 1999, personal communication). Its basidiomes were flabelliform, somewhat fleshy, caespitose or forked above the base, and growing from roots; microscopically, this had gloeocystidia, and spores that were hyaline, faintly amyloid, broadly ellipsoid or subglobose, and smooth (Lodge *et al.*, 2001, Fig. 12). This previously undescribed species differs from *Dichopleuropus* in lacking dextrinoid dichophyses in the tramal tissues, which is a major distinguishing feature of *Dichopleuropus*. Sequencing of the nuclear DNA 5.8S, ITS2, and the 5′-end of the 28S (LSU) regions by K.-H. Larsson and E. Larsson (Goteborg, Sweden, 2000, personal communication) indicated that this fungus (PR-5100) had affinities with taxa in the *Lachnocladiaceae*, which is consistent with the hypothesized placement of *Dichopleuropus* (Boidin *et al.*, 1998).

DNA sequences did not resolve all taxonomic problems. The placement of a group of fungi that macroscopically resembled *Stereum*, *Thelephora* and *Dichopleuropus*, and typified by collections from both Puerto Rico and Venezuela, remains unresolved. Their nuclear DNA sequences did not match any of those of the 170 taxa covering the major homobasidiomycete groups studied by Larsson and Larsson (Goteborg, Sweden, 2000, personal communication).

Some of the fungi collected by the group included species other than basidiomycetes. The most notable of these was a new resupinate genus and species of ascomycete, *Rogersonia striolata* Samuels & Lodge, that was mistaken for a corticiaceous fungus in the field. The new genus was closely related to *Hypomyces* in its stromatal morphology, but there was no indication of a fungal host, the apical discharge mechanism was absent from the asci, the spores were single-celled and broadly ellipsoid rather than two-celled, fusiform and apiculate; and the transverse striations on the ascospores of *Rogersonia* are otherwise unknown in the *Hypocreales*. Other additions to the *Hypocreaceae* included several new parasitic species of *Hypomyces* that were collected on polypores (Poldmaa *et al.*, 1997). An undescribed species of *Camarops* (*Xylariaceae*) which changed the normally grey pore surface yellow was found on vigorously growing *Tinctoporellus epimiltinus* (Berk. & Br.) Ryvarden.

Biogeographic Affinities

Some intriguing biogeographic patterns emerged from the agaric families that were examined most thoroughly (Lodge *et al.*, 2001). These patterns gave some

indication of centres of origin or speciation for certain genera, subgenera and sections. The two families that received the most attention were the *Hygrophoraceae* and *Entolomataceae*.

Hygrophoraceae

More than one-third of the 66 species and varieties identified in the *Hygrophoraceae* have been found only in the Greater Antilles (Lodge *et al.*, 2001; Table 4.3). A quarter of the species and varieties of *Hygrophoraceae* in the Greater Antilles have also been reported by Pegler (1983) from the Lesser Antilles. Only a few species are restricted to the Caribbean islands (both Greater and Lesser Antilles), but 17% are found scattered throughout the Caribbean Basin (Mexico, Central America, northern South America, and the Greater and Lesser Antilles; Table 4.3). A smaller percentage of species extend far into South America through the Lesser Antilles, or are absent from the Lesser Antilles (Table 4.3). The Neotropical elements in this family are represented primarily by *Hygrocybe* species in sections *Firmae* and *Coccineae*, and two species of *Hygroaster*. The Neotropics may be a centre of recent speciation for section *Firmae* since the greatest number of species are found there (Cantrell and Lodge, 2001; Lodge *et al.*, 2001).

Section *Firmae* is characterized by having dimorphic spores and basidia. Only one species in Section *Firmae* is pantropical, *H. hypohaemacta* (Corner) Pegler; it is also the only species that is found in moist as well as wet forests and as far north as Texas. At least three species in section *Firmae* are known from Mexico, including *H. hypophaemacta* (J. Garcia, Ciudád Victória, 2000, personal communication). It is significant that there has been only one possible report of a species in section *Firmae* from Costa Rica (C. Ovreboe, Edmond, Oklahoma, 2000, personal communication) despite extensive collecting there. Costa Rica and neighbouring parts of Central America are geologically young (approximately 3 million years old), whereas Mexico, parts of the Antilles and South America are much older. Their rarity in Central America suggests that species in section *Firmae* generally have poor dispersal and colonizing abilities, which may contribute to genetic isolation among populations on different islands or in different regions, and subsequent speciation.

Other taxa in the *Hygrophoraceae* appear to have a temperate origin, such as species in *Hygrocybe* subgenus *Hygrocybe* (Lodge *et al.*, 2001). Cantrell and Lodge (2000) described two new varieties of temperate species in this subgenus, *Hygrocybe calyptriformis* var. *domingensis* S.A. Cantrell & Lodge, and *Hygrocybe konradii*, var. *antillana* S.A. Cantrell & Lodge. These species may have reached the Caribbean recently. Species in subgenus *Hygrocybe* may disperse and colonize better than species in subgenus *Pseudohygrocybe*, section *Firmae*. While the Caribbean populations of *H. calyptriformis* and *H. konradii* differ by one or two morphological characters from their temperate relatives, greater dispersal and

Table 4.3. Geographic ranges are given for 63 species of *Entolomataceae* and 66 species and varieties of *Hygrophoraceae* that have been identified from the Greater Antilles. The number and percentage of species known from a given geographic range are presented (GA, Greater Antilles; LA, Lesser Antilles; SA, South America, and NA, North America). The Caribbean Basin includes Central America, northernmost South America (Trinidad and Venezuela) and the Antilles.

Range	Species of *Entolomataceae*	% of all species *Entolomataceae*	Species and varieties of *Hygrophoraceae*	% of all species *Hygrophoraceae*
GA	26	41.3	25	37.9
GA and LA	8	12.7	2	3.0
Caribbean Basin	10	15.9	11	16.7
GA, LA, and SA	0	0	7	10.6
GA and SA	3	4.8	4	6.13
Africa	34	4.8	0	0
Pantropical	2	3.2	1	1.56
New World	0	0	0	0
NA	9	14.3	2	3.0
NA and Europe	2	3.2	5	7.6
N. Temperate	0	0.0	4	6.1
Worldwide	0	0	5	7.6

colonization abilities in this subgenus may preclude the degree of genetic isolation needed to form a separate species. Other species with otherwise north temperate distributions also appear in the Greater Antilles, for example, *Hygrocybe caespitosa* Murrill and *Hygrocybe ovina* (Fr.) Kühner from North America, and *Hygrocybe* cf. *mucronella* (Fr.) P. Karst. from Europe, the latter differing from European collections in having broader spores.

Entolomataceae

Almost half the 63 species of *Entolomataceae* examined were apparently restricted to the Greater Antilles (Table 4.3). While species in various genera in this group were represented, there was a preponderance of *Alboleptonia* (Baroni and Lodge, 1998), *Claudopus* and *Pouzarella* species with highly restricted distributions (Lodge *et al.*, 2001). In contrast, three of the five *Rhodocybe* species were scattered throughout the Caribbean Basin. Less than a third (29%) of the species of *Entolomataceae* in the Greater Antilles were recorded by Pegler (1983) from the Lesser Antilles. While only a few species of *Entoloma* and *Leptonia* are found in both the Greater Antilles and South America below the Caribbean Basin (e.g. *Entoloma dragonosporum* (Singer) Horak and *Entoloma lowyi* (Singer)

Horak; Table 4.3), the closest apparent relatives of many species in the Greater Antilles are found in South America (Baroni *et al.*, 1997), and only two species, *Alboleptonia stylophora* (Berk. & Br.) Pegler and *Entoloma virescens* (Berk. & Curt.) Horak, have pantropical distributions. Neotropical collections of *A. stylophora*, however, are strikingly paler than the yellow forms found in the palaeotropics (E. Horak, Jamaica,1999, personal communication). Only a few species, such as *Inocephalus murraii*, *Leptonia incana* (Fr.) Gill and *Pouzarella foetida* Mazzer extend from North America or the North Temperate Zone into the Greater Antilles, but some eastern North American species have a sibling species in the Greater Antilles (Baroni *et al.*, 1997). The most surprising disjunct distributions found in the *Entolomataceae* in the Greater Antilles were those of *Inocephalus lactifluus* and *Inopilus inocephalus* from Madagascar (Baroni *et al.*, 1997). The pattern of disjunct populations of species and sibling species pairs in East Africa or Madagascar and the Caribbean or eastern Neotropics has similarly been found among ferns (Moran and Smith, 1999).

Ectomycorrhizal fungi

The island of Hispaniola has the easternmost extent of native pine in the Caribbean, *Pinus occidentalis* Swartz, which is an endemic species. Many of the ectomycorrhizal fungi found in the Dominican Republic on Hispaniola, for example *Strobilomyces confusus* Singer, are also found in south-eastern USA. Therefore, the presence of *Suillus albivelatus* Smith, Thiers & O.K. Miller among the collections was surprising, since it was known previously only from Idaho and the Pacific Northwest in the USA (Smith *et al.*, 1965; Bessette *et al.*, 1999). Collections from the Dominican Republic have been identified as *Lactarius rubrilacteus* A.H. Smith & Hesler, known previously from Washington to California, the Rocky Mountains from Idaho to New Mexico, and Mexico. Recent identifications of *Lactarius* collections from the Dominican Republic (A. Methven, Charleston, Illinois, 2000, personal communication) confirmed the occurrence of western North American disjuncts in the Greater Antilles. In addition to *L. rubrilacteus*, the western North American disjuncts included *Lactarius deliciosus* (Fr.) S.F. Gray var. *areolatus* A.H. Smith (Alaska to California, the Rocky Mountains from Idaho to New Mexico, and Mexico), and *Lactarius scrobiculatus* (Fr.) Fr. var. *canadensis* (A.H. Smith) A.H. Smith (Alaska east across Canada, south along the Pacific Coast to California, the Rocky Mountains from Idaho to Colorado, and Mexico) (Lodge *et al.*, 2001).

The possibility of an accidental introduction of western North American ectomycorrhizal fungi to Hispaniola cannot be ruled out without molecular data, but north-western North America is an unlikely source for an introduction, and the foresters in the Dominican Republic reportedly never brought rooted pines into the country. Alternatively, some of these western North American disjuncts might well be the remnants of ancient distributions that

extended south through the Rocky Mountains into the mountains of Mexico, Belize, northern Honduras and Guatemala, and east to the Greater Antillean islands. The island of Hispaniola was closer to northern Central America 35–65 million years ago than it is now (Hedges, 1992), which could have facilitated colonization by ectomycorrhizal fungi from the mainland; but more recent dispersal (not more than 23–25 million years ago) to the islands is more likely to have occurred based on the palynological history of pine in the Caribbean (Lodge *et al.*, 2001).

Summary and Conclusions

Although classification of all the collections from the Basidiomycetes of the Greater Antilles Project was not complete at the time of writing, it was clear that original estimates of the number of species and previously undescribed taxa in the Greater Antilles were conservative. Molecular data did not resolve all the taxonomic problems, but they were of great assistance in placing most of the new, as well as previously described, species into the correct genus and family. Molecular data were also crucial in establishing new genera.

A surprisingly high proportion (between one-third and one-half) of the species of *Hygrophoraceae* and *Entolomataceae* were apparently restricted to the Greater Antilles, with relatively little overlap between the Greater and Lesser Antilles, and pantropical species were rare. The biogeographical origins of basidiomycetes in the Greater Antilles are varied, but include South American and eastern North American elements, as well as African and western North American disjuncts. Some of the disjunct populations may be remnants of ancient distributions, whereas some of the species complexes in the *Hygrophoraceae* appear to have diversified recently. It is not known how fast basidiomycete fungi evolve, but many of the reptiles and amphibians of the Antilles that were once thought to have evolved tens of millions of years ago have arisen instead since the ice ages tens of thousands of years ago (James D. Lazelle, Guana Isl. BVI,1999; S. Blair Hedges, Orcas Island, Washington, USA, 2000, personal communications).

Acknowledgements

This work was made possible by grant DEB-95–25902 to the State University of New York College at Cortland from the National Science Foundation, Biotic Surveys and Inventories Program, and a joint venture agreement with the USDA-Forest Service, Forest Products Laboratory. In addition to the authors, the primary research group included Drs J. Carranza, K.K. Nakasone, K.-H. Larsson, R.E. Halling, E. Horak, Orson K. Miller Jr, P. Roberts, L. Ryvarden, R. Vilgalys and Mr A. Nieves-Rivera. Many other institutions and non-govern-

mental organizations provided matching funds and support which greatly facilitated the research, including the USDA-Forest Service's International Institute of Tropical Forestry (IITF), particularly the International Forestry Program, and NSF grant BSR-8811902 to the Terrestrial Ecology Division of the University of Puerto Rico and IITF in support of the Luquillo Experimental Forest Long Term Ecological Research Site in Puerto Rico. Molecular sequencing by R. Vilgalys and J.-M. Moncalvo, with funding from the National Science Foundation grants DEB-9708035 and DEB-9408347, 'The Agaricales: Molecular Systematics and Evolution of Mushrooms', was instrumental in classifying some of the unknown species. We thank our cooperators in the Dominican Republic, especially Sr Andrés Ferrer of the Fundación Moscoso Puello, Sra C. Cassanova and the staff of Fundación Plan Sierra, Fundación Progressio, Ing. Milciedes Mejía and Sra Daisy Castillo of the Jardín Botánico, Dr Raphael M. Moscoso, and the National Park Service. We also thank Ms Tracey Commock and the Institute of Jamaica, Natural History Division for assistance in Jamaica; Dr Carolyn Rogers of the USGS, the Maho Bay Ecotourist Resort, and the Virgin Islands National Park Service on St John, USVI; and the Conservation Agency and the Falconwood Foundation for support while working on Guana and Tortola Islands. We are eternally grateful to Ms Pat Catterfeld of the Research Foundation of SUNY-Cortland and L.A. Barley for taking care of a myriad of details in support of our research. Many people outside our research team assisted us with identifications (Drs D. Boertmann, R. Courtecuisse, G. and L. Guzmán, T. Laessøe, A. Methven, G. Mueller, D. Pegler, D. Reid and G. Samuels), and DNA sequencing (E. Larsson, J.-M. Moncalvo and J. Spatafora).

References

Baroni, T.J. and Lodge, D.J. (1998) Basidiomycetes of the Greater Antilles I: new species and new records of *Alboleptonia* from Puerto Rico and St John, USVI. *Mycologia* 90, 680–696.

Baroni, T.J., Lodge, D.J. and Cantrell, S.A. (1997) Tropical connections: sister species and species in common between the Caribbean and the eastern United States. *McIlvainea* 13, 4–19.

Benjamin, C.R. and Slot, A. (1969) Fungi of Haiti. *Sydowia* Ser.II., 23, 125–163.

Berkeley, M.J. and Curtis, M.A. (1868) Fungi Cubenses (Hymenomycetes). *Journal of the Linnean Society, Botany* 10, 280–392.

Bessette, A.E., Roody, W.C. and Bessette, A.R. (1999) *North American Boletes*. Syracuse University Press, Syracuse, New York.

Boidin, J., Mugnier, J. and Canales, R. (1998) Taxonomie moleculaire des *Aphyllophorales*. *Mycotaxon* 66, 445–491.

Cantrell, S.A. and Lodge, D.J. (2000) Hygrophoraceae (Agaricales) of the Greater Antilles. *Hygrocybe*, subgenus *Hygrocybe*. *Mycological Research* 104, 873–878.

Cantrell, S.A. and Lodge, D.J. (2001) *Hygrophoraceae* of the Greater Antilles, Section *Firmae*. *Mycological Research* 105, 215–224.

Cantrell, S.A., Lodge, D.J. and Baroni, T.J. (2001) Basidiomycetes of the Greater Antilles Project. *The Mycologist* (The Mycologist 15: 102–112).

Ciferri, R. (1929) *Micoflora Domingensis*. Estación Agronómica de Moca, Republica Dominicana, Seri B – Botanica No. 14, J.R. Vda. García, Sucesores, Santo Domingo, Dominican Republic.

Decock, C. and Ryvarden, L. (2000) Studies in Neotropical polypores. 6. New resupinate *Perenniporia* species with small pores and small basidiospores. *Mycologia* 92, 354–360.

Dennis, R.W.G. (1950) An earlier name for *Omphalina flavida* Maubl. & Rangel. *Kew Bulletin* 5, 434.

Dennis, R.W.G. (1951a) Some *Agaricaceae* of Trinidad and Venezuela. Leucosporae: Part 1. *Transactions of the British Mycological Society* 34, 411–480.

Dennis, R.W.G. (1951b) *Lentinus* in Trinidad B.W.I. *Kew Bulletin* 5, 321–333.

Dennis, R.W.G. (1951c) *Agaricaceae* referred by Berkeley and Montagne to *Marasmius*, *Collybia* and *Heliomyces*. *Kew Bulletin* 6, 387–410.

Dennis, R.W.G. (1953) Some West Indian collections referred to *Hygrophorus* Fr. *Kew Bulletin* 8, 253–268.

Dennis, R.W.G. (1970) *Fungus Flora of Venezuela and Adjacent Countries*. Kew Bulletin Additional Series 3, HMSO, London.

Earle, F.S. (1906) Algunos hongos cubanos. *Información Anual Estación Central Agronomica Cuba* I, 225–242.

Earle, F.S. (1909) Genera of North American gill fungi. *Bulletin of the New York Botanical Gardens* 5, 375–462.

Gilbertson, R.L. and Ryvarden, L. (1987) *North American Polypores*, Vols 1 and 2. Fungiflora, Oslo, Norway.

Hedges, S.B. (1992) Caribbean biogeography: molecular evidence for dispersal in West Indian terrestrial vertebrates. *Proceedings of the National Academy of Sciences USA* 89, 1909–1913.

Hennings, P. (1898) Fungi jamaicensis. *Hedwigia* 37, 277–282.

Hesler, L.R. (1967) Entoloma in southeastern North America. In: *Beihefte zur Nova Hedwigia*, Heft 23. J. Cramer, Stuttgart, Germany.

Hesler, L.R. and Smith, A.H. (1963) *North American Species of Hygrophorus*. The University of Tennessee Press, Knoxville, Tennessee.

Hjortstam, K. (1990) Corticoid fungi described by M.J. Berkeley: II. Species from Cuba (West Indies). *Mycotaxon* 39, 415–424.

Legon, N.W. (1999) A mycological expedition to Puerto Rico. *The Mycologist* 13, 58–62.

Lodge, D.J. (1996a) Fungi of Puerto Rico and the US Virgin Islands: a history of previous surveys, current status, and the future. In: Figueroa Colón, J.C. (ed.) *The Scientific Survey of Puerto Rico and the Virgin Islands*. NY Academy of Sciences, New York, pp. 123–129.

Lodge, D.J. (1996b) Microorganisms. In: Regan, D.P. and Waide, R.B. (eds) *The Food Web of a Tropical Forest*. University of Chicago Press, Chicago, pp. 53–108.

Lodge, D.J. and Pegler, D.N. (1990) The *Hygrophoraceae* of the Luquillo Mountains of Puerto Rico. *Mycological Research* 94, 443–456.

Lodge, D.J., Baroni, T.J., Miller, O.K. Jr and Halling, R.E. (2001) Emerging biogeographic patterns among macrobasidiomycete fungi in the Greater Antilles. In: Zanoni, T. (ed.) *Biogeography of Plants in the Greater Antilles*. New York Botanical Gardens, New York.

Miller, O.K. Jr and Lodge, D.J. (2001) New species of *Amanita* from the Dominican Republic, Greater Antilles. *Mycotaxon* (in press).

Miller, O.K. Jr, Lodge, D.J. and Baroni, T.J. (2000) New and interesting ectomycorrhizal fungi from Puerto Rico, Mona, and Guana Islands. *Mycologia* 92, 558–570.

Moncalvo, J.-M., Lutzoni, F.M., Rehner, S.A., Johnson, J. and Vilgalys, R. (2000) Phylogenetic relationships of agaric fungi based on large subunit ribosomal DNA sequences. *Systematic Biology* 49, 278–305.

Moran, R. and Smith, A. (1999) Phytogeographic relationships between Neotropical and African-Madagascan Pteridophytes. *Proceedings of the XVI International Botanical Congress, 1–7 August 1999, St Louis, Missouri*. Abstracts, addendum, pp. 9–10.

Murrill, W.A. (1910) The *Polyporaceae* of Jamaica. *Mycologia* 2, 183–197.

Murrill, W.A. (1911a) The *Agaricaceae* of Tropical North America. I. *Mycologia* 3, 23–36.

Murrill, W.A. (1911b) The *Agaricaceae* of Tropical North America. II. *Mycologia* 3, 79–91.

Murrill, W.A. (1911c) The *Agaricaceae* of Tropical North America. III. *Mycologia* 3, 189–199.

Murrill, W.A. (1911d) The *Agaricaceae* of Tropical North America. IV. *Mycologia* 3, 271–282.

Murrill, W.A. (1915) *Tropical Polypores*. Published by the author, New York.

Murrill, W.A. (1920a) Light coloured resupinate polypores I. *Mycologia* 12, 77–92.

Murrill, W.A. (1920b) Light coloured resupinate polypores II. *Mycologia* 12, 299–308.

Murrill (1921a) Light coloured resupinate polypores III. *Mycologia* 13, 83–100.

Murrill (1921b) Light coloured resupinate polypores IV. *Mycologia* 13, 171–178.

Nakasone, K., Burdsall, H.H. Jr and Lodge, D.J. (1998) *Phanerochaete flava* in Puerto Rico. *Mycologia* 90, 132–135.

Pegler, D.N. (1983) *Agaric Flora of the Lesser Antilles*. Kew Bulletin Additional Series 9, HMSO, London.

Pegler, D.N. (1987a) A revision of the Agaricales of Cuba 1. Species described by Berkeley & Curtis. *Kew Bulletin* 42, 501–585.

Pegler, D.N. (1987b) A revision of the Agaricales of Cuba: 2. Species described by Earle and Murrill. *Kew Bulletin* 42, 855–888.

Pegler, D.N. (1988) A revision of the Agaricales of Cuba: 3. Keys to families, genera and species. *Kew Bulletin* 43, 53–75.

Pegler, D.N., Lodge, D.J. and Nakasone, K.K. (1998) *Macrocybe* gen. nov. (*Tricholomataceae*, tribus *Tricholomatae*). *Mycologia* 90, 494–504.

Poldmaa, K., Samuels, G.J. and Lodge, D.J. (1997) Three new polyporicolous species of *Hypomyces* and their *Cladobotryum* anamorphs. *Sydowia* 49, 80–93.

Rodríguez Gallart, C.A. (1989) Estudios en los macromicetos de la Republica Dominicana. I. *Moscosoa* 5, 142–153.

Rodríguez Gallart, C.A. (1990) Estudios en los macromicetos de la Republica Dominicana. II. *Moscosoa* 6, 202–212.

Rodríguez Gallart, C.A. (1997) Estudios en los macromicetos de la Republica Dominicana. III. *Moscosoa* 9, 145–153.

Ryvarden, L. (1984) Type studies 13. Species described by Berkeley and other authors 1855–1886. *Mycotaxon* 20, 329–363.

Ryvarden, L. (1985) Type studies in the Polyporaceae 17. Species described by W.A. Murrill. *Mycotaxon* 23, 169–198.

Ryvarden, L. (2000a) Studies in neotropical polypores. 2: a preliminary key to neotropical species of *Ganoderma* with a laccate pileus. *Mycologia* 92, 180–191.

Ryvarden, L. (2000b) Studies in Neotropical polypores 5. New and noteworthy species from Puerto Rico and Virgin Islands. *Mycotaxon* 74, 119–129.

Ryvarden, L. (2000c) Studies in neotropical polypores. 7. *Wrightoporia* (Hericiaceae, Basidiomycetes) in tropical America. *Karstenia* 40, 153–158.

Ryvarden, L. (2002) Studies in Neotropical polypores. 8. Poroid fungi from Jamaica – a preliminary check list. *Mycotaxon* (in press).

Schmit, J.P., Murphy, J.F. and Mueller, G.M. (1999) Macrofungal diversity of a temperate oak forest: a test of species richness estimators. *Canadian Journal of Botany* 77, 1014–1027.

Smith, A.H., Theirs, H.D. and Miller, O.K. (1965) The species of *Suillus* and *Fuscoboletinus* of the Priest River Experimental Forest and Vicinity, Priest river, Idaho. *Lloydia* 120–138.

Stevenson, J.A. (1970) *Fungi of Puerto Rico and the American Virgin Islands*. Publication 23, Reed Herbarium, Baltimore, Maryland.

Swartz, O.P. (1788) *Nova genera et species plantarum*. Holmiae, Stockholm, Sweden.